THE NESTING AND THE LIFE EQUATION OF THE WISCONSIN BOB-WHITE

BY PAUL L. ERRINGTON

The nesting of the bob-white has already been exhaustively studied in the course of Stoddard's (1931) classic work in the south. He was also concerned with the working out of a coherent life equation through a study of the various mortality factors determining population levels for the species. Ecological research on the northern bob-white has been the aim of the quail investigation (1929-'32) which was established at the University of Wisconsin by the Sporting Arms and Ammunition Manufacturers' Institute and the U. S. Biological Survey. Although in a great many respects the Georgia life history findings hold true for northern as well as for southern quail, yet the north has very much its own problems, its own factors of shifting values. The Wisconsin nest studies, then, do not represent a northern attempt to duplicate in entirety Stoddard's program, but advantage has been taken of his methods.

Cock quail the season of 1931 began calling "bob-white" about the last of March (earliest record March 26) and were calling quite frequently by mid-April. At this time the birds were loosely pairing up, but still attached to the old coveys. The flocking habit was weakening, however, and by late April the covey as a social unit had generally disintegrated. I suspect that many of the pairings were not of any degree of permanence before May 1. Eleven of the sixty-nine Wisconsin quail nests on which I have personal data were calculated to have received their first eggs between May 2 and May 10, but one of the University bird banders got an egg in a trap April 27! It may be that the nesting season of 1931 was somewhat early over Wisconsin quail country as a whole, for the quail came through the mild, almost snowless winter in splendid condition. Populations that barely squeeze through a long winter of hunger may not be ready for laying by the fore part of May.

The topographic location of nests is largely determined by the location of nesting cover available, mainly bluegrass (*Poa*, June grass). Unless pastured, burnt, or mowed off, this bluegrass occurs in the most satisfactory density and proximity to feeding grounds along roadsides and field fencerows, where twenty-five and fourteen nests were found respectively. It also occurs prominently in orchards and ornamental plantings, in which were situated ten more nests. Three nests were built in woodland bluegrass patches. Fourteen were in hay fields, one on a pastured hillside, one on a sandy knoll, and

one on the edge of an erosion gully. Thirty-two were within a few yards of cultivated fields.

Thirty-three of the sixty-nine nests were in nearly pure bluegrass stands; seventeen in bluegrass mixed with other grasses (quack grass, timothy, etc.). In midsummer almost any herbaceous vegetation, open yet affording concealment, may be utilized. Nine nests had backgrounds of alfalfa, six of timothy, one of panic grass (*Panicum*), one of mixed wild barley (*Hordeum*) and pigeon grass (*Setaria*), and two were on virtually bare ground but roofed over with mint stems (*Monarda*) in one case and with bluegrass stems in the other. The last mentioned was constructed half-way up a steep cut bank entirely from materials carried to the spot and skillfully woven to form a roof.

Fifty-two out of sixty-five were either roofed over or in vegetation sufficiently thick to provide the equivalent of roofing; eleven were partially concealed from most angles; and two had no top covering whatever. The nest openings did not face any constant direction. Eleven were exposed to the southeast; nine to the east; nine to the north; eight to the south; eight to the southwest; five to the northwest; five to the northeast; four to the west; and eight had no discernible exposure. Thiry-seven nests were in places sun-lit during most of the day; five in morning sunlight; nine in afternoon; eighteen in places briefly or diffusely illuminated, exemplified by alfalfa fields or open woodlands.

Nest sites were well chosen as to drainage, twenty-seven being adjudged excellent; twenty-eight good; ten fair; and three poor. The three poorly drained nests were located in low spots in hay fields, certainly not because of necessity, for there was abundant alternative cover.

The exact positions for eighteen nests (principally May nests) were chosen with reference to tufts of dry grass, weed stems, fallen branches, saplings, small briar canes, etc., which may serve to supplement nesting cover not too inviting early in the season. That mechanical obstruction to large moving dangers such as trampling domestic animals as well as concealment may likewise be gained is indicated by the establishment of fourteen nests under fence wires; eight at the base of posts; one under a stump; one partly under a log; and one under a low conifer.

Whether there is a definite evolutionary tendency for quail to nest more and more under fence wires and in similarly protected places, I cannot say. An inimical agency selective enough against non-conformers might ultimately modify the nesting habits of the species. An agency of this kind we might have in the mowing machine.

The prevalent practice in my observational areas is to mow both roadsides and hayfields during the last half of the main nesting season, a practice responsible for fourteen out of my thirty-five nest failures. In only one instance did a hay-field nest hatch before the hay was cut; in two instances adults remained on mowed-over nests to hatch out the young. I might observe parenthetically that a cheap and practical iron rod designed by Peterson (1931) for attachment to mowing machines has received favorable comment as a device to flush incubating Hungarian Partridges from hay-field nests, thus enabling the farmer to stop the team before the nests are destroyed.* It has not been tested on quail.

Man was closely responsible for the failure of eight other nests, viz., three desertions on account of human snoopers; two desertions presumably because of the activities of workmen near by; one nest crushed by a saddle horse (?); one by a wagon wheel; and one accidentally hoed out of a cultivated tract. A cow cropped away the covering of another nest, as a result of which something filched the eggs. Three nests were deserted from unknown causes, including one maybe through my fault.

Direct predaceous influences were detected in the destruction of five nests: three by striped ground squirrels (*Citellus tridecemlineatus*); one by a skunk (*Mephitis*); and one by a dog. Three were broken up without any perceptible clue, and another under circumstances that seemed to point to fox squirrel. The preceding losses given in this paragraph relate to live nests; most of the clutches exposed by mowing were soon rifled, especially when abandonment left the eggs in plain sight. Two mowed-over clutches were devoured in the typical slobbery canine manner; others disappeared in a way suggestive of crows.

Adult mortality during the nesting season? The incubating bird of one of the mowed-over nests was hit by the sickle, but the seriousness of the injury is not known. Several farmers have told me of having killed or injured quail while mowing. The past two summers four banded quail were known to have been killed in steel traps set for ground squirrels on one suburban property. The remains of an old bird (a kill of about three days) were found in front of a hatched-out nest; the evidence indicated housecat as strongly as anything, but it was very inconclusive. Contemporaneous studies on raptor food habits, particularly Great Horned Owls, Cooper's Hawks, Marsh

*Information on other flushing devices of later origin may be obtained from the Iowa Fish and Game Department, Des Moines, or from American Game Association, Investment Building, Washington, D. C.

Hawks, and redtails disclosed no summer quail leakage save for a single July individual taken by a Great Horned Owl. I was unable to obtain many data on the summer food habits of mammalian predators (foxes, Mustelidae, etc.), so the question of their role as enemies of adult bob-whites at this season will have to remain open.

In one case a cock took over nesting duties some days after incubation had been started by the hen. Does this hint the demise of the hen? Altogether, three of the twenty-four incubating birds, the sex of which could be identified, were males. The other two began incubation upon completion of the clutches, a normal occurrence (Stoddard, 1931).

I am not ready to hazard an opinion as to the likelihood of the three mysteriously abandoned nests representing mortality. While my data reveal no preponderance of desertions at any time of the season, quail have been noted to exhibit no great fidelity to their nests until incubation has begun, and may be expected to desert during the laying period at practically any time that something happens of which they do not approve. As the hatching date of the eggs draws near the birds become less "touchy" about disturbances, even some (mowing) which must seem cataclysmic to them.

Clutches appear to have equally good prospects for hatching if laying is begun either previous to June 1 or delayed until the latter part of the month.

Clutches began		Hatched	Lost	Remarks
First half of May,	14	8	6	2 deserted
Last half of May,	7	4	3	2 deserted
First half of June,	13	2	11	3 deserted, 5 mowed over
Last half of June,	8	5	3	1 deserted, 2 mowed over
First half of July,	5	3	2	1 deserted, 1 mowed over
Last half of July,	3	3	0	
August,	3	2	1	

A broad statement might be made that the early clutches are the largest and that later ones decrease progressively until the approach of fall. This does not imply that a pair will raise more than one brood in a season; it is simply the manifestation of repcated attempts to bring forth young after breaking up or desertion of previous nests.

Complete clutches began		Average number of eggs
First half of May,	11	19.2
Last half of May,	6	16.6
First half of June,	9	17.0
Last half of June,	6	14.2
First half of July,	5	13.8
Last half of July,	3	11.3
August,	2	9.0

Complete data were not obtainable on the thirty-four successful nests of the sixty-nine, but of these eight hatched in June; nine in the first half of July; four in the last half of July; three in the first half of August; four in the last half of August; and two in September. The continued June and July hatching, despite the widespread mowing operations of these months, is due to the advantageous locations of the nests started before luxuriant growths of timothy and alfalfa tempted the birds away from the comparatively safe but restricted fencerow bluegrass.

Very late clutches in addition to being small may also hatch imperfectly, and the young may be hopelessly backward to meet cold weather. My latest brood had three live chicks (of ten eggs, six didn't pip and one chick died beside the nest) hatched September 24, 1930. Occasionally an observer encounters half-grown quail, or smaller, along in November, but the evidence is scant that many of them get much farther. I would judge that a quail must be hatched by September 1 in order to have a fighting chance to survive a moderately rigorous winter.

Thirty-one nests produced 420 living young or an average of 13.6 per nest. Left in these nests were forty-five, or 9.7 per cent, unhatched eggs, most of which were sterile or contained dead embryos. The usual cause of death of embryos appeared to be chilling; for example, seven out of a clutch of seventeen were killed at the point of hatching apparently by water collecting in the bottom of a nest during a heavy rain. Sometimes, too, individual eggs were noticed to be uncovered by the incubating bird. One chick was partially eaten by small animals (ants?) in an opened shell. Two young were found dead on the ground in the vicinity of the nests.

The quantitative measurement of chick mortality so far has been quite too much of a problem for me, but a few observations illustrate how heavily peril weighs upon the young in the early helpless stages. Two chicks (15 and 20 grams) became wedged and died under (not inside) the wire floor of a cage bird trap. Another was cut in two by a mower sickle. I have been told of chicks that couldn't climb out of a plowed furrow. The body of a newly hatched quail chick was retrieved from a domestic chicken in a farmyard. Stoddard mentions cats attracted by peeping of hatching young, and I have strong evidence of a striped ground squirrel bringing ruin to a nest under similar conditions. The counterpart of Stoddard's (1931 and unpublished) terrifically destructive ants I have not discovered in the North.

Let us, by the juggling of what data we have, endeavor to secure

some kind of evaluation of some factors governing bob-white populations.

The central portion of one of my observational areas at Prairie du Sac, Wisconsin, gave an accurate census of seventy-three quail at New Years, 1930. At New Years, 1931, the census was 184, an increase of 152 per cent. The central portion differed to no radical degree from the surrounding territory, either with respect to quail populations or environmental types, so it is thought that errors due to summer ingress or egress of birds should compensate for each other.

The quail of this area lost no more than 5 per cent from New Years, 1930, up to the breeding season, thus leaving sixty-nine birds as stock. A sex tally on 305 Wisconsin bob-whites, mainly random specimens and birds trapped for banding, shows but 42.3 per cent females. This ratio applied to sixty-nine birds gives twenty-nine females, and hence a maximum of twenty-nine pairs. The percentage of non-breeding females in another area (University Marsh Farm, Madison, Wis.) was computed to be 15 per cent.* If we may be permitted to transpose this percentage of non-breeding (?) females to the Prairie du Sac area, the twenty-nine pairs would be lessened by four.

If the twenty-five breedings pairs nest early in May and are so fortunate as corresponding early nesters actually studied, they will be 57 per cent successful in their initial attempts. Their 14.3 successful nests will average 19.2 eggs, of which 9.7 per cent will not hatch. This gives 248 live young and leaves 10.7 pairs to make renesting attempts.

Of the 10.7 unsuccessful pairs two-thirds or 7.1 pairs (on basis of advancement of clutches when lost) are in condition to continue their laying with but brief interruption after the breaking up of their first nests. Their chances for success will be the same as for the first and 57 per cent or four nests will succeed and 3.1 will fail. The average clutch will be 16.6 eggs minus 9.7 per cent (eggs not hatching) or sixty live young for the four pairs.

There are 6.7 pairs left, which if they raise young at all are not destined to raise an early brood. Of these, let us say, five pairs are still able to renest the first half of June. To no slight extent on ac-

*University Marsh Farm census of eighty-nine quail, March 2, 1930. A loss of three (assumed, but based on some data) up to breeding time leaves eighty-six birds. General banding records for area show 46.2 per cent females or a ratio of forty females to forty-six males. This gives an excess of six cocks. An observed July, 1930, excess of twelve whistling unmated cocks may then be indicative of six non-breeding females or fifteen per cent of the forty. Possible sources of error: unknown spring-summer reduction of hens or influx of cocks from outside.

count of mowing, only 15.4 per cent or .8 nests will succeed, and the population will be increased by twelve live young.

The six unsuccessful pairs may be rather worn out by this time but will probably try again in July or August. In this event 68.4 per cent or 4.1 nests will succeed, which high percentage will be offset by the smaller clutches and will give us only forty-eight young.

The season is now over, and, assuming no adult mortality, after a total of forty-three trials, 23.2 out of the twenty-five pairs were able to hatch out broods varying in size from four to twenty-one. The total number of chicks (248+60+12+48) equals 368, or an average of 14.7 young for the twenty-five pairs (15.9 for the 23.2) despite the failure of 44 per cent of the nesting attempts. The percentage of loss shown by the 1929-31 data is 51 per cent, though the fourteen nests spoiled by mowing may not represent the correct proportion, as several were found only as rendered conspicuous by removal of the cover. Since the observed 51 per cent loss is not beyond comparison with the hypothetical 44 per cent of the Prairie du Sac area, nor the observed average of 13.6 young per successful nest with the hypothetical average of 15.9, we therefore have some grounds for accepting the Prairie du Sac calculations as indicative of about what happens. Discrepancies between calculations and observational data may be attributed principally to fortuitous hatching variations in the individual nest data lumped to obtain averages.

The best estimate I can make on summer losses to adult birds, based upon inferences from unsolved nest desertions and upon detached bits of data from mowing and traffic accidents and a very few predator kills, is 10 per cent or seven birds, which would leave sixty-two adult survivors for Prairie du Sac at the conclusion of nesting. Seven birds from the population would mean 2.5 breeding pairs, one of which might be lost before reproduction could be consummated. This would cut the 23.2 more or less successful pairs to 22.2.

If we now correct our calculated 15.9 chick per successful nest average to the observed 13.6 average and multiply by the above calculated 22.2 successful pairs, we get a probably more representative total of 302 chicks instead of 368. We then have for the Prairie du Sac area 302 chicks plus sixty-two adults or a population peak of 364 individuals. The fact that some broods have been suffering mortality two months or so before others hatch should not upset our reasoning.

How does a population of 364 become reduced to 184 by New Years? This brings us to a realm of tantalizing unknowns into which no one, of whom I am aware, has penetrated very deeply. True, glimpses of juvenile mortality are now and then obtained, but quan-

titative data on this phase of the bob-white's life history are almost utterly lacking. From here on we must assign increasingly arbitrary values to our factors.

Let us reduce the average size of each brood from 13.6 to ten to allow for the post-nesting juvenile losses up to the time that part-grown young are frequently seen in late summer or early fall. Broods from seven to fifteen are common (all of same size and with one or two adults—not the heterogeneous mixtures of later coveys), and an average of ten may perhaps be as logical as any. Eighty chicks would thereby be eliminated at semi-helpless stages, the victims of accident, vicissitudes of weather, and hungry creatures from which hiding ability and feeble running or flight powers might not always enable them to escape.

By September 15, we may call our population 62 old birds and 222 young of divers sizes. One hundred birds are to die in the next three and one-half months, to be apportioned largely among pot-shooting rabbit hunters in November and December, Cooper's Hawks, and to some extent among Great Horned Owls and migrating Sharp-shinned Hawks.

Losses from Prairie du Sac Great Horned Owls from October to January ran at a rather uniform rate of 1.5 per cent for the 1929-'31 quail population, so five birds might be subtracted from the doomed hundred. An allowance for partly fledged youngsters that succumb to the first October ice storm and for losses from accidents and possibly from Marsh Hawks, foxes, and other of the less efficient avian predators and those mammals which occasionally capture birds lacking resourcefulness, experience, or full physical capacity to take care of themselves might be set at fifteen, though this value is unsubstantiated by actual data.

The residual mortality of eighty birds can be attributed to the pot-hunters, Cooper's Hawks, and Sharp-shinned Hawks. I am inclined to doubt that the sharp-shins get many, for they seem to follow their own food supply (warblers, finches, etc.) southward, and I have never observed them attending quail. A loss of five may be charged to sharp-shins, for want of a better figure.

Winter observations on 473 quail for an average of seventy days disclosed a Cooper's Hawk loss that could be established at 2 per cent and a pot-hunting loss of 1.7 per cent. Both loss rates should be much higher in the fall when the young quail are more numerous and less wary, equally with respect to their native and to their human enemies. If we assume that the ratio of Cooper's Hawk kills to poaching kills is still 2:1.7 for the fall (in probability illegal shooting does far more

damage than Cooper's Hawks in the fore part of November when the opening of the rabbit hunting season draws out all sorts of irresponsibles), we can put down forty birds for the Cooper's Hawks and thirty-five for the pot-hunters. This very conveniently accounts for the remaining 75 missing bob-whites, however remote it may be from the truth.

Thus we have improvised, for a better than average Wisconsin environment a bob-white life equation, which, while it limps badly toward the end, is still an equation and as such is conceivably superior to no equation at all. It at least illustrates a method.

By this we may gain something of an idea how a thriving population ascends in one year from 73 to 184 mature birds. Apart from the direct losses occasioned through man, it is to be remarked that the annual mortality from what we call natural causes is extremely high—extremely high in terms of slow-breeding animals like man himself.

Examined more carefully, the losses take on a less formidable aspect. It is to be seen that nature is most prodigal with the lives of those in which a minimum is invested. The destruction of a dozen newly laid eggs early in the season may cost the species practically nothing. A dead day-old chick has not as much significance to the species as a dead bird that has reached breeding age, irrespective of the potentialities of the chick. Lastly, let it be made clear that a given environment, year in, year out, can support only about so many birds. When the species has filled up the tolerable environmental niches, something has to befall the surplus—unless the environment is improved to accommodate it.

If any one season in the Wisconsin bob-white's life history is supremely critical, it is winter. The complete failure of a summer's nesting need not be as disastrous to the species as a wretched winter survival. The trivial 5 per cent wintering loss given for the Prairie du Sac coveys should not be mistaken for an index as to what commonly occurs. To coveys forced by agricultural practices, emergencies, and the like, to live under adverse environmental conditions—such as prevail throughout much if not most of the Wisconsin quail range—winter means 50 per cent losses or higher, even up to annihilation (Errington 1933).

No, it is not the cold except as the cold kills the starving and those otherwise subnormal. Nor have I yet reason to believe that it is largely the snow, except as snow covers up the food supply and so promotes starvation; nor have I reason to believe it is to any extent a matter of predaceous enemies except where the birds are very much

handicapped, as by territorial deficiencies, starvation, wounds, or possibly disease. The major part of the wintering losses, according to the data at hand, can be laid to inadequacy or unavailability of high grade food or to lack of cover which prevents the birds from finding immediate refuge in case of danger (Errington 1931a, 1931b, 1933). There are many large quail-vacant spaces where some intelligently distributed fencerow brush or a few shocks of corn may mean all the difference between no coveys and perhaps two or three.

TABULAR RECAPITULATION OF THE LIFE-EQUATION OF THE WISCONSIN BOB-WHITE

on three square miles east of Prairie du Sac, January 1, 1930 to January 1, 1931.

Date	Items and Computations	Gain	Loss	Current population
Jan. 1, 1930	Census of quail in area			73
May 1 (pairing)	5% loss since New Years (based on data)		4	69
	General Wisconsin quail sex ratio is 57.7 males to 42.3 females. 42.3% of 69=29 females or 29 possible pairs. Non-breeding females (?), 15% (calculated in another area). 15% of 29 is 4, which subtracted from 29 leaves 25 pairs			
May 1-15 (first nesting attempt	General data show 57% success of nests begun at this time, an average clutch of 19.2 eggs and an average loss of 9.7% eggs through failure to hatch. 57% of 25 initial attempts give 14.3 hatchings. 14.3×19.2=275 eggs. 275 minus 27 (the 9.7%) leaves 248 living young	248		317
May 16-31	Two-thirds of the 10.7 unsuccessful pairs or 7.1 are in condition for prompt renesting (clutches were lost while incomplete). Nests begun at this time are 57% successful, average 16.6 eggs. The 9.7% of unhatched eggs may be considered constant for the summer. 57% of 7.1 attempts give 4 hatchings. 4×16.6=66 eggs. 66 minus 6 (9.7%) leaves 60 young	60		377
June 1-15	Five of the 6.7 unsuccessful pairs (on basis of some data) may be able to renest now. Nesting attempts are only 15.4% successful (destruction through mowing high), average 17 eggs per nest. 15.4% of 5 attempts give .8 hatchings. .8×17=14 eggs. 14 minus 2 (unhatched) leaves 12 young	12		389

Date	Items and Computations	Gain	Loss	Current population
June 16-30 July, and August	The 6 unsuccessful pairs try again during the summer. Their attempts are 68.4% successful, average 12.9 eggs. 68.4% of 6 attempts give 4.1 hatchings. 4.1×12.9=53 eggs. 53 minus 5 (9.7%) leaves 48 young	48		437
	The above calculations give 368 young for the 23.2 eventually successful nests or an average of 15.9 chicks. For this average (which is likely too high to be representative) we may substitute an average of 13.6 actually arrived at from field studies.			
	15.9 (cal. av.)×23.2 (calc. successful pairs)= 368			
	13.6 (obs. av.)×22.2 (corrected calc. successful pairs)*=302			
	Difference due to correction 66 yg.		*66*	371
Summer	Adult losses (calc. on basis of mowing, traffic, and misc. mortality data)		7	364
	Small chick losses (almost wholly arbitrary but based on fragments of weather, predator, and misc. mortality data)		80	284
Fall	Illegal shooting (arbitrary, but based on some data)		35	249
	Mammalian and slow avian predator losses, accidents, misc. (arbitrary)		15	234
	Horned owls (well supported by data)		5	229
	Migrant sharp-shinned hawks (arbitrary)		5	224
	Cooper's hawk (arbitrary, but based on some data)		40	184
Jan. 1, 1931	Census of quail on area			184

*Loss of a pair assumed before reproduction was accomplished.

References

Errington, Paul L.
1931a. The bob-white's winter food. American Game, Vol. 20, pp. 75-78, September-October.
1931b. The bob-white's winter cover. American Game, Vol. 20, pp. 90-93, November-December.
1933. The wintering of the Wisconsin bob-white. Trans. Wisconsin Acad. Sci. Arts and Letters, Vol. 28, pp. 1-35.
Peterson, A. J.
1931. An iron rod that beats any law. American Game, Vol. 20, September-October, 1931, page 72.
Stoddard, H. L.
1931. The bob-white quail (New York, Scribner's).

Iowa State College,
Ames, Iowa.